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Are small rodents key promoters of ecosystem restoration in harsh environments? A case study of abandoned croplands on Mongolian grasslands

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ABSTRACT

We focused on the potential contribution of fossorial rodents to recovery of degraded abandoned Mongolian croplands. From field observations and the literature, we determined that plant litter and soil crusting were the main factors preventing establishment or growth of the perennial grass *Elymus chinensis* (Poaceae) on these croplands. We hypothesized that small fossorial rodents such as Mongolian gerbils promote grass establishment and growth by clearing litter and destroying crusts. We designed a path model linking number of burrows to patch size and plant volume of *E. chinensis*. As we hypothesized, small rodents increased the patch size of *E. chinensis* through reduction of litter cover. However, unexpectedly, we could not find significant effects on *E. chinensis* via crust thickness. Our results suggest that litter removal by the rodents gave *E. chinensis* suitable space that was free of competitors; this allowed expansion of the *E. chinensis* patches. Any effect of soil crusting on plant volume could not be explained simply by the variables we used, probably because some other mechanism, such as temporal variation in the crust, was involved. We demonstrate that small rodents are key agents in the recovery of degraded grasslands.

1. Introduction

Desertification—decline in land quality in arid environments—is a problem closely linked to abandonment of croplands (Rey-Benayas et al., 2007; Zhao et al., 2005). Abandoned croplands occupy about 436,000 ha of the Mongolian steppe (National Scientific Office of Mongolia, 2007). On the Mongolian steppe, as in other countries, abandoned croplands are widely covered with hard-crusted soils as a result of agriculture (Awadhwal and Thierstein, 1985; Ludwig et al., 1995). The vegetation on this land is characterized by standing dead plants or their materials on the soil surface, and under this litter there has been no recovery since the land was abandoned. The perennial grass *Elymus chinensis* grows in monospecific patches in wheel ruts where the soil crust and the litter have been destroyed or excluded, implying that the establishment or growth of *E. chinensis* is suppressed by crusted soil or litter in these croplands.

The physical crust itself affects the establishment or growth of *E. chinensis*, because it prevents seed germination through mechanical resistance (Awadhwal and Thierstein, 1985), as well as by hampering gaseous exchange by seeds (Taylor, 1992) and decreasing infiltration (Edwards and Larson, 1969; Roulier et al., 2002). Plant litter also affects the establishment or growth of *E. chinensis* because some of the forb litter is standing and not decomposed, and thus tends to trap the seed rain above the ground and intercept elongating *E. chinensis* roots underground (Huber-Sannwald et al., 1998; Humphrey and Pyke, 2001; McConnaughay and Bazzaz, 1992; Schmid and Bazzaz, 1992).

There are burrows of fossorial rodents throughout the croplands of the Mongolian steppe. The rodents in these arid areas have habits that modify their environment: digging soil, stamping the soil surface, grazing plants and seeds, and hoarding food (Lortie et al., 2000; Whitford and Kay, 1999). Through these activities, ground-dwelling rodents modify the microtopography, soil structure, and plant structure (Komonen et al., 2003; Schauer, 1987; Sherrod and Seastedt, 2001). For example, the amount of soil removed around and in their colonies is eight times greater than that in grasslands without colonies (Ceballos et al., 1999), and patches of bare ground are found near the nests of the rodents (Dean and Milton, 1991; Komonen et al., 2003). It is therefore reasonable to expect that these rodents remove or destroy the crust and reduce the volume of plant litter lying on the surface. We hypothesized that fossorial rodents promote the establishment and expansion of *E. chinensis* on abandoned croplands by clearing litter and destroying the soil crust.

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Because of its high palatability for livestock and high productivity, *E. chinensis* is considered to be one of the recovery indicator species in degraded cropland (Li, 1978). *Elymus* may be useful for site restoration by serving as a stepping stone to a community that includes other species of perennial grasses and shrubs (Hironaka and Sindelar, 1973; Jones, 1998). Therefore, colonization with *E. chinensis* instead of dead litter, as a first step, would encourage recovery at these sites.

2. Materials and methods

2.1. Site description

Our investigations were conducted in a buffer zone in Hustai National Park (HNP; 47°50′ N, 106°00′ E, elevation 1100–1840 m), located 100 km west of Ulaanbaatar. Average monthly temperatures vary greatly between −23 °C in January (coldest month) and 20 °C in July (hottest). The annual average temperature is 0.2 °C. The mean annual precipitation in HNP is 232 mm, most of which is received in summer. Hustai National Park covers approximately 600 km^2, including grasslands with shrubs, birch forests, rivers, sand dunes, and abandoned croplands. The croplands had been used for wheat until 2000. Since their abandonment, they have been covered by bare ground with standing dead *Artemisia mongolica*, its materials on the soil surface, and a few living seedlings. The impact of livestock grazing on these abandoned croplands seems to have been small because of the unpalatable, poor nature of the vegetation and the exclusion of livestock from HNP over the last 15 years for conservation purposes. The species of small rodent found most frequently on the croplands is the Mongolian gerbil (*Meriones unguiculatus*); Brandt voles (*Microtus brandti*) and hamsters (*Phodopus* spp.) are found, but rarely.

2.2. Model design

The hypothesized cause-and-effect relationships among variables are summarized in Fig. 1. Small rodents could affect *E. chinensis* via their effects on plant litter. Plant litter in this study was defined as standing dead plants and their materials on the soil surface. We nominated two response variables for *E. chinensis*: patch size and plant volume. We defined an *E. chinensis* patch as a discrete unit with a spatial pattern of homogeneous vegetation surrounded by bare ground or dead litter. In the first pathway of the model, small rodents would affect plant litter by grazing on and removing it. The Mongolian gerbils feed mainly on the annual herb *Artemisia* (Agren et al., 1989). Small rodents create patches of bare ground near their nests through foraging and food hoarding (Dean and Milton, 1991; Komonen et al., 2003). Indeed, at our study sites we found that litter was brought to the gerbils' nests and accumulated in their holes. In the second pathway, plant litter would affect the patch size and volume of *E. chinensis* because some of the litter of *A. mongolica* is standing and not decomposed; it thus tends to trap the seed rain above the ground and intercept elongating *E. chinensis* roots underground (Huber-Sannwald et al., 1998; Humphrey and Pyke, 2001; McConnaughay and Bazzaz, 1992; Schmid and Bazzaz, 1992).

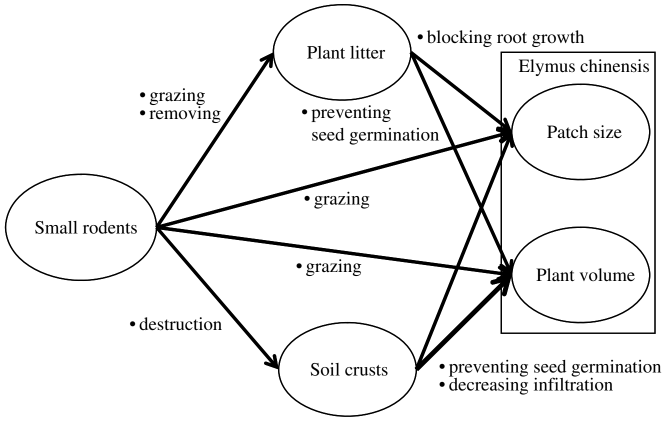

Fig. 1. Our hypothesized conceptual model linking disturbance by small rodents to *E. chinensis*, including direct and indirect paths via plant litter and soil crusts. Text inside each ellipse describes variables. Path arrows represent predicted cause-and-effect relationships. For each arrow, conceivable factors derived from the literature are given (see model design).

Small rodents could affect the patch size and volume of *E. chinensis* directly by grazing. The small rodents in these croplands are all herbivorous and graze *E. chinensis* (Agren et al., 1989).

Small rodents could also affect the patch size and volume of *E. chinensis* by their disturbance of the soil crust. In one pathway, the rodents would remove or destroy the crust. Ground-dwelling small rodents modify the microtopography and soil structure by burrowing, digging, and stamping (Schauer, 1987; Sherrod and Seastedt, 2001). In the other pathway, the physical crust itself would affect the patch size and volume of *E. chinensis*, because it prevents seed germination through mechanical resistance (Awadhwal and Thierstein, 1985), hampering gaseous exchange of seeds (Taylor, 1992) and decreasing infiltration by as much as 50% (Edwards and Larson, 1969), especially in the deeper soil layers (Roulier et al., 2002). In contrast, destruction of the physical crust to make a rough surface may positively affect the lodgment of seeds (Prasse and Bornkamm, 2000). Break-up of crusts has resulted in a high potential sorghum yield in a simulation model (Daba, 1999). These effects are magnified in dry areas, because mechanical impedance by the crust is increased by high levels of evaporation (Taylor, 1992). Because *E. chinensis* is drought-sensitive (van Staalduinen and Anten, 2005), we can expect destruction of the crusts by small rodents to work in favor of this plant, because its rhizomes have a deeper underground distribution than those of *A. mongolica*. Digging by the woylie (*Bettongia penicillata*) in undisturbed, highly water-repellent woodland soils in Australia appears to favor water infiltration (Garkaklis et al., 1998).

Huber-Sannwald et al. (1998) showed that *Elymus lanceolatus* was influenced by the presence of neighboring species much more than by local nutrient enrichment. Because our preliminary tests showed no differences in nutrient status between soils occupied by rodent colonies and those not occupied, we did not include soil nutritional properties in our model.

2.3. Sampling design

In mid-July 2007 we established four plots in cropland situated in the northern part of HNP. Each plot was 50 m × 50 m and contained a matrix of *E. chinensis* patches and dead *A. mongolica* plants. Within the four 0.25-ha plots, we examined a total of 30 patches. To formulate a description of patch structure, in each patch we measured the patch length and width. Because the patches were either round or elongated, patch size was calculated from patch length and width by an elliptic formula. We laid out three 1-m × 1-m quadrats within each patch and recorded the plant cover and height of *E. chinensis* in each quadrat. Plant volume was calculated from plant cover and height. In each patch, we located the positions of inactive or active burrows separately by using a Global Positioning System receiver (Garmin Inc., Taiwan). The numbers of abandoned burrows reflected the former influence of rodents, and the numbers of active burrows reflected the current influence. However, because of the rodents' frequent migration we could not judge the importance of each type of burrow separately in terms of the extension of patches, so we combined active and inactive burrows. To estimate the impact of rodents on plant patches, we defined a mean active range of the Mongolian gerbil (11.75-m radius from the home burrow) after Agren et al., 1989. With the aid of ArcMAP 9.2, we then counted the number of burrows within a buffer radiating out 11.75 m from the border of each sampling patch. The average litter cover within each patch was recorded. The thickness of the soil crust was measured at three points in each patch as this soil property can be modified by small rodents.

2.4. *Statistical analysis*

Our hypothesis included the direct effects of small rodents on *E. chinensis* patches and indirect effects via the modification of litter cover or soil crust thickness (Fig. 1). We used a path analysis to test whether our hypothesized paths described actual relationships among variables and to determine the relative importance of direct and indirect effects. This analysis calculates and outputs the path coefficients (analogous to standardized partial regression coefficients) and the cause–effect relationships among input variables. In our diagram, numbers of burrows, cover of litter, and crust thickness were independent variables, and patch size and volume of *E. chinensis* were dependent variables. In the analysis we used only burrows within a 11.75-m radius of patch. Before its use in the modeling procedure, the number of burrows was log-transformed to correct for bias in the distribution.

We performed structural equation modeling procedures to assess model fit. First, we calculated the observed and predicted covariances between pairs of all variables and from the final parameter estimation. We then compared the observed matrix with the predicted covariance matrix. We used a robust index, the NFI (Normed Fit Index), proposed by Bentler and Bonett (1980), to judge goodness of fit. We calculated this index for the full model and for the reduced model, from which we removed variables one by one. We then selected the full model with the highest NFI (0.964). NFI varies between 0 and 1, with values >0.9 usually considered an indication of good agreement (Hatcher, 1994). Thus, this value was interpreted as indicating good fit between the observed and predicted covariances. We used the t statistic to assess the significance of individual path coefficients. All differences among comparisons with $P \leq 0.05$ were considered significant. These analyses were performed with Statistica 5.5—SEPATH (Systat Inc.).

3. Results

The variables used and their ranges are shown in Table 1. The number of burrows had a significant negative effect on litter cover ($P = 0.008$) but no significant effects on patch size ($P = 0.20$), plant volume ($P = 0.95$), or thickness of crust ($P = 0.95$; Fig. 2). Increased litter cover was associated with a significant decline in patch size ($P = 0.04$), but there was no relationship with plant volume ($P = 0.67$). There were no significant relationships between crust thickness and either patch size ($P = 0.83$) or volume ($P = 0.44$). Thus, the number of burrows was positively related to patch size indirectly via litter cover ($-0.40 \times -0.34 = 0.136$). The amounts of unexplained variability of crust thickness and plant volume were very high.

Table 1
Variables sets used in the path models.

Variable	Mean	SD
Explanatory variables		
Burrow density within patch (/m^2)	0.09	0.11
Density of old burrows within patch (/m^2)	0.38	0.53
Number of burrows within active range	7.57	5.67
Litter coverage (%)	17.97	8.40
Thickness of crust (mm)	5.17	3.99
Objective variables (*Elymus* patches)		
Patch size (m^2)	11.75	11.45
Plant height (cm)	20.89	4.71
Plant coverage (%)	23.37	6.75
Density of plant by volume (/m^2)	480.25	154.82

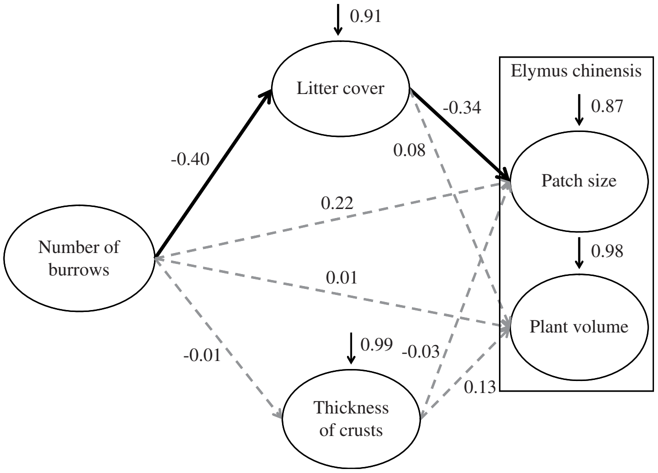

Fig. 2. Path analysis among variables assumed to be involved in direct and indirect effects of small rodents on *E. chinensis* patches. The numbers near each arrow represent standardized path coefficients. Bold and dotted arrows indicate significant and insignificant effects, respectively, at $P = 0.05$. Unexplained variability is indicated by the vertical arrows above each ellipse.

4. Discussion

Although very few studies have examined the roles of small rodents in land recovery, Martin (2003) reviewed the evidence for the importance of these rodents in the rehabilitation of inhospitable environments. For example, the pocket gopher (*Thomomys talpoides*) affects the progression of succession after volcanic eruptions (Andersen and MacMahon, 1985). Brant's whistling rat (*Parotomy brantsii*) created small, fertile patches that encouraged plant colonization in an abandoned open-cut mine (Desmet and Cowling, 1999). However, to our knowledge, our report is the first to find that small rodents contribute to the recovery of abandoned degraded croplands. We found a significant effect of small rodents on patch size of *E. chinensis* through litter clearing, but we did not find an effect through soil crust disruption. The observed effect of small rodents on patch size was not direct, but acted indirectly through an effect on litter cover.

Small rodents increased the patch size of *E. chinensis* through a series of negative relationships between number of burrows and litter cover, and between litter cover and patch size. As the height of standing dead litter of *A. mongolica* ranges from 10 to over 100 cm in these croplands, this litter may be a nuisance to small rodents. Small rodents such as gerbils and voles favor short grasslands (Zhong et al., 1985) so that they can detect and avoid predators (Komonen et al., 2003). McConnaughay and Bazzaz (1992) showed that the presence of artificial neighbor root systems reduced plant growth through the fragmentation of physical space. Kleijn and Van Groenendael (1999) reported that the high level of plasticity of the rhizomes of *Elymus repens* enables the plant to selectively intrude into favorable, bare microsites. We suspect that clearing of litter by rodents gave *E. chinensis* suitable space (i.e., bare ground) that was free of competitors and had more light for germination; the *E. chinensis* patches could therefore expand into these spaces. Also, the fact that gerbils select mainly the seeds of annual dicots as food (Wang and Zhong, 1998; Zhong et al., 1985) may assist in the progressive succession to perennial grass.

Litter cover affected the patch size of *E. chinensis* but not the aboveground volume. Removal of litter by small rodents might have given *E. chinensis* favorable space that was free of competitors; it may also have caused the plant to allocate more resources to the roots. Wang et al. (1999) found strong negative relationships between vegetative shoot biomass and rhizome biomass in *E. chinensis*. Ba et al. (2006) showed that *E. chinensis* allocates more biomass to the shoots and less to the roots when the number of neighbors is increased.

The presence of small rodents did not directly affect the patch size and aboveground volume of *E. chinensis*. The intensity of grazing of these rodents is low, judging from the small proportions of areas that had been grazed at our sites. Being a rhizomatous species, *E. chinensis* may be able to strongly compensate for grazing by small rodents and make up for any losses (van Staalduinen and Anten, 2005).

Small rodents did not affect the patch size or plant volume of *E. chinensis* through changes in the soil crust thickness. The big unexplained value in Fig. 2 implies that other factors determine crust thickness. Generally, crust strength is affected by moisture, drying, rainfall intensity and duration, soil texture, type of clay, bulk density, and organic matter (Awadhwal and Thierstein, 1985). Thus, crust thickness varies spatially and temporally (Arndt, 1965; Zhenghu et al., 2003). At our sites, not a temporal but an accumulative effect on the crust may have affected *E. chinensis*. Seed production of *E. repens* is usually poor, so the plant's main mode of reproduction is by rhizome (Parish and Turkington, 1990). Thus, the blockage of root spaces with dead plants could be critical to the patch size of *E. chinensis*, but crusting may not be critical, because at our study site the rhizomes grew transversely under the crust, at about 5– 10 cm depth.

Mongolian gerbils fluctuated seasonally in density and population (Liu et al., 2007). The growth rate of the population peaked in early spring and showed a sudden decline from summer to autumn (Liu et al., 2007). These rodents prefer the green parts of plants (Y. Yoshihara, personal observation), but they have no choice but to eat dead litter in the early spring, when there is no green feed. Thus, the grazing by the rodents on the litter may have a more positive effect on *E. chinensis* in spring.

In recent years, ecosystem engineering has received attention as a means to address conservation or management problems (Boogert et al., 2006; Byers et al., 2006; Crain and Bertness, 2006). Fossorial rodents modify the soil's physical and chemical properties through activities such as burrowing, grazing, and urinating, thereby affecting the distribution of plant species; this is an example of ecosystem engineering (Jones et al., 1994). The effects of ecosystem engineers on the environment depend on the nature of that environment. In general, organisms tend to have positive ecosystem effects in more harsh environments through the amelioration of physical stress (Crain and Bertness, 2004, 2006). Thus, ecosystem engineers can be important facilitators of restoration in degraded environments like these abandoned croplands in arid environments.

In conclusion, small rodents could contribute to the recovery of grassland by clearing litter and thus encouraging the expansion of *E. chinensis* patches. Managers involved in conservation planning may be concerned about population explosions of small rodents and the potential negative impact of the rodents' heavy grazing after the recovery of grasslands. However, the rodents would be likely to disappear from revegetated areas because of their need for short grasslands (Zhong et al., 1985). The augmentation or manipulation of these engineering species creates a window of opportunity for achieving revegetation goals. Our results demonstrate that fossorial rodents are key agents in the recovery of degraded lands.

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